FRESHWATER HYBODONT SHARKS FROM THE LOWER CRETACEOUS OF THAILAND

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Abstract

The lower Cretaceous of Thailand has yielded isolated teeth of eight hybodont genera, including *Hybodus*, *Lonchidion*, *Thaiodus* and *Heteroptychodus.* They are distributed in two successive assemblages, the first one from the Sao Khua Formation (Neocomian), and the second one from the Khok Kruat Formation (Aptian), with only two genera in common between these two assemblages, *Hybodus* and *Heteroptychodus*. These sharks show a wide range of diet and many of them were restricted to freshwater environment and thus endemic to the Khorat Plateau. The distribution of *Thaiodus* and *Heteroptychodus,* known in other Asian locations, may be explained by a mode of life similar to that of the modern sawfish *Pristis perotteti*.

Introduction

New data from the Early Cretaceous of Thailand show an unexpected diversity of hybodont sharks in freshwater environments, first in the Sao Khua Formation (Neocomian), and then in the Khok Kruat Formation (Aptian), with a total of 8 different genera recorded so far.

Geological settings

The Khorat Group is a set of sandstones, clays and freshwater limestones deposited during the Mesozoic in Northeastern Thailand (and parts of adjacent

Laos and Cambodia). It ranges in age from the Late Jurassic (Phu Kradung Formation) to the Cenomanian (Maha Sarakham Formation), and its total thickness is nearly 3200 m. Hybodont shark remains have been so far retrieved from the Phu Kradung Formation (Uppermost Jurassic), the Sao Khua Formation (Neocomian) and the Khok Kruat Formation (Aptian). This article will focus on the Sao Khua and Khok Kruat faunas.

Systematic description

Class: Chondrichthyes Huxley 1880
Subclass: Elasmobranchii Bonaparte 1838
Order: Hybodontiformes Maisey 1987
Family: Hybodontidae Owen 1846
Subfamily: Hybodontinae Maisey 1989
Genus: H*ybodus* Agassiz 1837
Hybodus sp. A

Occurences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

Because of space restriction, the precise description of the teeth can be found in Cuny et al. (2003). See also Fig. 1A-C.

Discussion

The density of the ornamentation of these teeth is reminiscent to that of *Hybodus brevicostatus* from the Wealden of Britain (Patterson, 1966). However, the teeth from Thailand are easily distinguished from those of *H. brevicostatus* by the much better developed main cusp and lateral cusplets and the absence of lingual nodes at the base of the crown. These teeth also show an ornamentation quite similar to those of *Hybodus* sp. described from the Upper Jurassic of Ethiopia (Goodwin et al., 1999), but again are easily distinguished on the basis of the first pair of lateral cusplets almost as high as the main cusp and the absence of fine, short non-branching ridges on the cutting edge. The teeth from Thailand, with their first pair of lateral cusplets

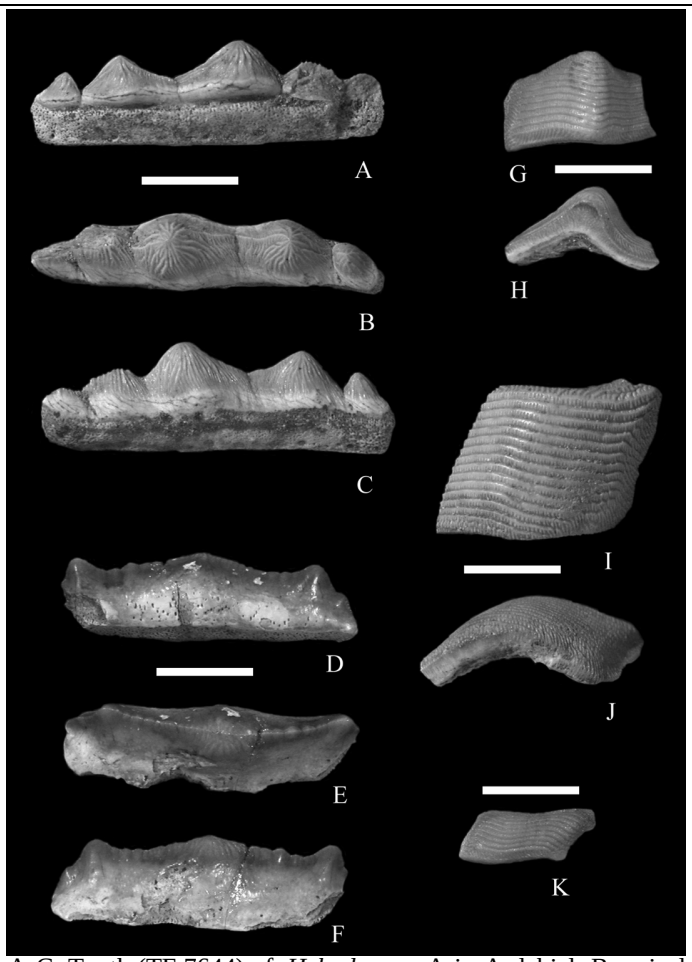

Fig. 1: A-C: Tooth (TF 7644) of *Hybodus* sp. A in A: labial, B: apical and C: lingual view. D-F: Tooth (TF 7646) of *Thaiodus ruchae* in D: labial, E: apical and F: lingual view. G-K: *Heteroptychodus steinmanni.* G-H: anterior tooth (TF 7647) in G: apical and H: labial view. I-J: lateral tooth (TF 7648) in I: apical and J: labial view. K: posterior tooth (TF 7649) in apical view. All scale bars: 5 mm. All the specimens come from Khok Pha Suam.

almost as high as the main cusp, appear to be fairly unique and probably belong to a new species.

Hybodus sp. B

Occurences: Phu Phan Thong, Nong Bua Lamphu province, Sao Khua Formation.

Description

See Cuny et al. (2003).

Family: Ptychodontidae Jaekel 1898
Genus: *Heteroptychodus* Yabe & Obata 1930
Heteroptychodus steinmanni Yabe & Obata 1930

Occurrences: Phu Phan Thong, Nong Bua Lamphu Province, Sao Khua Formation; Phu Wiang 1A, Khon Kaen Province, Sao Khua Formation; Phu Kum Khao, Kalasin Province, Sao Khua Formation; Phu Phok, Sakon Nakhon Province, Sao Khua Formation; Non Liam, Chaiya Phum Province, Sao Khua Formation; Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

See Cuny et al. (2003) and fig. 1G-K and 2E-F.

Discussion

The dentition can be reconstructed as follows: Anterior teeth (TF 7647, fig. 1G, H) with a well developed bulge not in the centre of the crown, large crushing lateral teeth (TF 7648, fig. 1I, J) with a moderately developed bulge, and small, flattened posterior teeth (TF 7649, fig. 1K). Some teeth might belong to juveniles (Fig. 2E).

This genus was hitherto known only from a handful of teeth found in the Lower Cretaceous of Japan (Yabe & Obata, 1930; Tanimoto & Tanaka, 1998). However, hybodont teeth attributed to the genus *Asiadontus* were reported from the Aptian-Albian of Kirghisia and Mongolia (Nessov, 1997). The ornementation of these teeth is very similar to that of *Heteroptychodus* and it is

likely that the two genera are synonyms. *Heteroptychodus* was thus present all around the Asian continent.

The teeth of *Heteroptychodus* differ from those of *Ptychodus* by a reduced marginal area and a denser pattern of parallel longitudinal ridges ornamenting the crown. The teeth with a well-developed bulge recall what is seen in *Ptychodus whipplei* (Williamson et al., 1993) or *P. rugosus* (Cappetta, 1987). The massive root, narrower than the crown, is also similar to that of *Ptychodus.* We therefore include *Heteroptychodus* in the family Ptychodontidae, which thus comprises two genera: *Heteroptychodus* and *Ptychodus,* as *Hylaeobatis* is now considered better included in the family Lonchidiidae (Batchelor & Ward, 1990; Rees & Underwood, 2002).

The teeth of the juveniles are more reminiscent of the ornamentation pattern of *Ptychodus* showing well-separated longitudinal ridges devoid of secondary ridges although the marginal area is still very reduced. The main difference however is the presence of one cusp on each of the ridges. However, if we compare with modern sharks possessing a grinding dentition, Reif (1976) has documented that the juveniles of the modern *Heterodontus* show a dentition that is not as grinding as that of the adult. It is therefore reasonable to think that this may have also been true of some Mesozoic hybodonts, although similar cusps, to the best of the knowledge of the authors, have never been reported in the genus *Ptychodus.* The presence of secondary ridges in *Heteroptychodus* appears to be size-related as labial ones are present only in the largest teeth. Their absence on juvenile teeth is therefore not surprising. The attribution of TF 7655 and similar teeth to a juvenile *Heteroptychodus,* which must be considered tentative, relies therefore on the hypothesis that their diet was different from that of the adults, and the fact that they share with the adult an ornamentation which is made of parallel longitudinal ridges with a reduced marginal area.

Family: *incertae sedis*
Genus: *Thaiodus* Cappetta, Buffetaut & Suteethorn 1990
Thaiodus ruchae Cappetta, Buffetaut & Suteethorn 1990

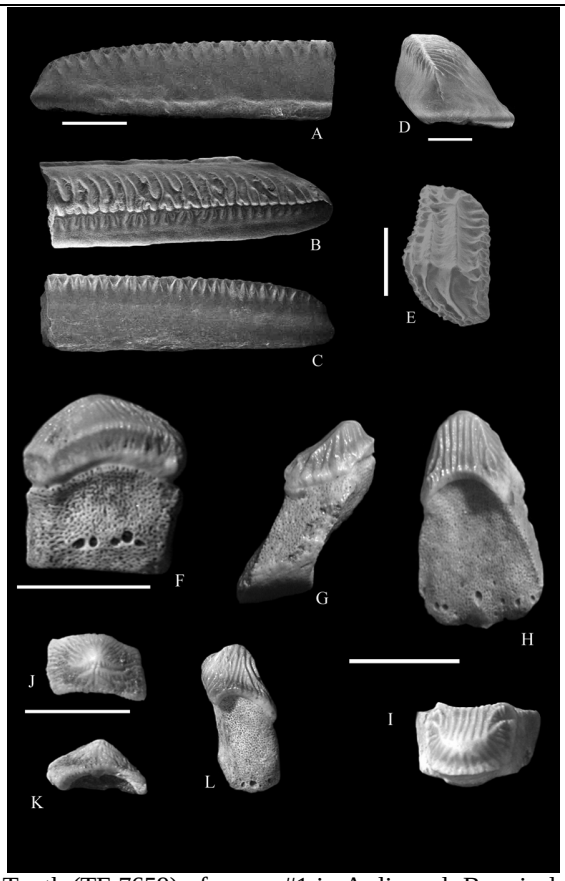

Fig. 2: A-D: Tooth (TF 7659) of genus #1 in A: lingual, B: apical, C: labial and D: mesial or distal view. E: tooth (TF 7655) of a juvenile *Heteroptychodus steinmanni* in apical view. F: Lateral tooth (TF 7650) of *Heteroptychodus steinmanni* in labial view. G-I: Tooth (TF 7657) of genus #2 in G: mesial or distal, H: lingual and I: apical view. J-L: Teeth of genus #3. J-K: TF 7651 in J: apical and K: lingual view. L: TF 7653 in lingual view. Scale bars: A-C, E: 1 mm, D: 0.5 mm, F-L: 5mm. All the specimens come from Khok Pha Suam.

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation; Ban Khok Kruat, Nakhon Ratchasima Province, Khok Kruat Formation.

Description

See Cuny et al. (2003) and fig. 1D-F.

Discussion

The teeth of *Thaiodus ruchae,* currently known only from Thailand and Tibet (Cappetta et al., 1990) show a unique morphology characterized mainly by the presence of irregular, obtuse, serrated denticles and a highly asymmetric crown, the lingual face being concave and flared basally while the labial face is gently convex. However, new material currently under study by Cappetta might indicate that the orientation of the teeth used in this work is wrong, the labial face being the lingual one and vice versa. Anyway, these characters clearly separate these teeth from those of any Hybodontidae, even if one accepts the broad definition of this family by Maisey (1989), which includes the genera *Palaeobates, Asteracanthus, Bdellodus, Acrodus, Egertonodus* and *Hybodus,* plus *Tribodus* (Brito & Ferreira, 1989; Maisey & de Carvalho, 1997) and *Priohybodus* (Duffin, 2001). The inclusion of *Thaiodus ruchae* into the Hybodontidae by Cappetta et al. (1990), not justified by the possession of shared derived characters, seems therefore unlikely. *Thaiodus,* probably, belongs to a family of its own.

New genus and species #1

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation

Description

See Cuny et al. (2003) and fig. 2A-D.

Discussion

The low crown profile and elongated shape of these crowns suggest that they formed crushing batteries, as in *Asteracanthus* (Rieppel, 1981) or *Acrodus* (Mutter, 1998). But unlike these two Hybodontidae, they share with the teeth of *Thaiodus ruchae* an asymmetric crown with a convex labial face and a basally flared lingual face. Moreover, both kinds of teeth share a mesio-distally

elongated crown. This strongly suggests that these two genera are closely related.

New genus and species #2

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

See Cuny et al. (2003) and fig. 2G-I.

Discussion

These teeth share with *Thaiodus ruchae* and genus #1 a convex labial face and a concave, basally flared lingual face. They are easily distinguished from the two previous taxa by a strong ornamentation and teeth that are moderately elongated mesio-distally. According to the small number of teeth available and their rather poor preservation, the heterodonty of this species cannot be assessed. Therefore, the phylogenetic relationships of genus #2 are rather difficult to ascertain, and we prefer to leave this genus in open nomenclature for the time being.

New genus and species #3

Occurrences: Khok Pha Suam, Ubon Ratchathani Province, Khok Kruat Formation.

Description

See Cuny et al. (2003) and fig. 2J-L.

Discussion

With only ten teeth at hand and no precise idea about the heterodonty pattern, the affinities of this new genus are rather difficult to decipher. Several characteristics recall the teeth of *Heteroptychodus:* the parallelogram to rectangular shape of the crown with a very high root showing a row of basal enlarged foramina, the basal surface of the root smaller than that of the crown, the presence of some ridges parallel to the longitudinal crest, and a crown which is arched in lingual and labial view. However, the small number of teeth

currently available makes the hypothesis of a relationship with *Heteroptychodus* difficult to ascertain. On the other hand, similarities in root morphology (Compare fig. 2H and L) may indicate that genus #2 and #3 are closer to each other than to *Heteroptychodus.* Pending the discovery of more material, we therefore prefer to leave this genus in open nomenclature.

Discussion and conclusion

The Khorat plateau has yielded a rich hybodont shark fauna, although it was deposited in a nonmarine environment. Moreover, the diversity of the Sao Khua Formation is even higher than reported here as new material, not yet described, seems to indicate the presence of three new taxa belonging to the family Lonchidiidae. The shark diversity in the Sao Khua Formation is thus similar to that of the Khok Kruat Formation.

The Thai hybodonts display a wide range of possible diets according to their dentition. *Hybodus* spp. and genus #2 were probably opportunistic feeders while the grinding dentition of *Heteroptychodus,* genus #1, and genus #3 indicate more durophagous sharks. Finally, the cutting dentition of *Thaiodus* suggests a diet mainly consisting of large, soft-bodied preys. These sharks thus represented an important and diverse component of the freshwater ecosystems of the Khorat Plateau.

Genera #1, #2, and #3 are so far endemic to the Khorat Plateau and likely to have been infeoded to freshwaters, hence their endemism. *Hybodus* possesses a worldwide distribution, but the exact affinities of the Thai material appear unclear due to a lack of material, except for *Hybodus* sp. A, which clearly belong to a new species that appears again to be endemic to the Khorat Plateau. *Thaiodus* on the other hand is known both from the Khorat Plateau and Tibet, where it has been found in a deltaic environment (Cappetta et al., 1990). This shark was therefore able to tolerate some changes in salinity. Finally, *Heteroptychodus* has the largest distribution, having been recorded in Thailand, Japan, Kirghisia, and Mongolia (Yabe & Obata, 1930; Nessov, 1997; Tanimoto & Tanaka, 1998). The palaeobiogeographic distribution of the two latter taxa is difficult to explain if we consider these sharks as strictly confined to freshwaters. However, Maisey (1989) suggested that many hybodont genera (*Hamiltonichthys, Hybodus, Lissodus)* were in fact euryhaline. Such a mode of life would explain the distribution of *Heteroptychodus* and *Thaiodus* around the Asian continent, as it would explain how these hybodonts were able to follow the coastline to invade several freshwater systems. A similar strategy is seen

today among the sawfish *Pristis perotteti*, which has colonized several lakes along the Atlantic coast of Central and South America (Thorson, 1982). Following a similar pattern, the spreading of *Thaiodus* and *Heteroptychodus-Asiadontus* would have been favoured by the Late Aptian sea transgression (Averianov & Skutschas, 2000). However, as these sharks are unknown outside Asia, they were probably unable to face open water.

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